

FLUCTUATION OF A MARSH HABITAT AND THE REPRODUCTIVE STRATEGY OF THE YELLOW-HEADED BLACKBIRD

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ABSTRACT.— The Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) nests in marshes and is dependent on emergent vegetation for nest sites. Fluctuating water levels from year to year cause an increase or decrease in the amount of emergent vegetation and affect the time required for the vegetation to become suitable for nesting. Nests built in marshes are very susceptible to wind, rainfall, vegetation growth, and predation. Many nests are abandoned before being used and the mortality of eggs and young is high. The reproductive strategy of the Yellow-headed Blackbird has been selected for flexibility and opportunism to compensate for the unpredictability of the marsh situation.

Fluctuations in the physical environment can often cause dramatic changes in the local population sizes or reproductive strategies of organisms. The more potential the environment has for short-term change, the more flexible the resident-organisms must be. The marsh-nesting Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), whose breeding ecology and behavior has been extensively studied by Willson and Orians (1963), Willson (1966), and Orians and Christman (1968), is an organism that clearly demonstrates this flexibility. This study describes the fluctuation in some reproductive characteristics of a population of Yellow-headed Blackbirds in a marsh habitat over a six-year period and expands an earlier report (Lederer et al. 1975).

STUDY AREA AND METHODS

The study area is a marsh 500 m north of the Eagle Lake Field Station on the eastern shore of Eagle Lake, Lassen Co., California. The marsh is dependent on Eagle Lake for its water; a rising water table formed the marsh in 1968 (R. Ediger, pers. comm.).

This study was conducted from mid-May to late July from 1972 to 1977, inclusive. The marsh was censused for adult birds, nests, eggs, and young at least five times per week by walking about transects 25 m apart. Each nest was plotted on a map of the study area, marked with a numbered

tag, and the number of eggs and/or nestlings in it was recorded. Observations of the movements of the adult males and aggressive encounters between males were used to determine territorial boundaries. The size of the female population was estimated from the number of active nests and counting of adults. At the peak of the breeding period the surface area and depth of the marsh were measured. Weekly measurements of emergent vegetation height and density were made in several areas around the marsh.

Relationships between variables listed in Table 1 (Dimensions of marsh habitat) and Table 2 (Population and nesting data) were tested with linear regression or linear correlation analysis.

RESULTS

PHYSICAL DIMENSIONS OF THE MARSH.— Table 1 shows that the marsh increased in size and average depth each year from 1972 through 1975, but decreased in both dimensions in 1976 and 1977.

ADULT POPULATION AND TERRITORY SIZE.— Over the six years both the adult population and the number of territories showed an increase. Territory sizes varied. The only significant ($p < .05$) relationship found was a positive relationship between the surface area of the marsh and territory size.

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The sex ratio was very consistent over the years, being 2.95 to 3.10 females to males (\bar{x} = $3.03 \pm .07$).

NESTS, CLUTCH SIZES, AND FLEDGLINGS.—Active nests (many built were never used) produced a low mean of .03 fledged young per nest in 1977 to 1.70 in 1974. There is a significant ($p < .01$) negative correlation between the number of active nests and the average number fledged per active nest. There is also a significant ($p < .05$) negative correlation between the total number of nests and the average number of young fledged per active nest; and the ratio of active/total nests is significantly ($p < .005$) negatively correlated with the average number fledged per active nest. If the number of young fledged per active nest is the criterion of success, then 1974 was the most successful year.

SIZE OF MARSH AND FLEDGING SUCCESS.—There is a significant ($p < .05$) positive correlation between the surface area of the marsh and the number of fledglings per adult.

MORTALITY.—Known causes of mortality of eggs and young were abandonment, toppling into water, and predation by the raccoons (*Procyon lotor*) and coyote (*Canis latrans*). Weather-related mortality was apparent in 1974 when heavy rains occurred,

and severe storms in 1975 and 1976 destroyed large numbers of nests which contained eggs or young. Willson (1966) reported similar results. Mortality of fledglings is not known but may be at least 50 percent (Ricklefs 1973). There was extensive raccoon predation in 1977.

DISCUSSION

NEST SITES.—The number of Yellow-headed Blackbirds nesting in a habitat is strongly influenced by the adequacy of nest sites (Immelmann 1972, Willson 1966). Nests were placed in emergent vegetation about .3 m above the water and encompassed 8-70 stalks of *Scirpus* sp. (bulrush) and/or *Juncus* sp. (rush). Because *Scirpus* stalks are thicker and taller than those of *Juncus*, only 10-20 stalks of *Scirpus* could support a nest, but 30-50 stalks of *Juncus* were required. Often, both species were incorporated into the nest and its support. *Scirpus* and *Juncus* grew in shallower water and thus emerged and were available for nesting before *Scirpus*. But *Juncus* frequently proved to be too weak or too sparse, and the nests collapsed or were torn apart as the vegetation grew or the water level changed. Ellarson (1950) and Stevens (1937) (IN: Willson 1966) reported Yellow-headed

TABLE 1. Dimensions of marsh habitat.

	1972	1973	1974	1975	1976	1977
Surface area (hectares)	3.9	4.0	5.3	13.4	8.2	2.5
Average depth (meters)	1.1	.98	1.3	1.6	.8	.43

TABLE 2. Yellow-headed Blackbird population and nesting data.

	1972	1973	1974	1975	1976	1977
Adult population	25	85	83	71	137	202
Number of territories	8	28	28	24	44	66
Minimum-maximum territory sizes (m ²)	not measured	40-101	40-150	804-1500	20-225	7-188
Active nests	8	29	19	53	93	290
Empty nests	0	67	110	58	66	30
Total nests	8	96	129	111	159	320
Ratio of active/total nests	1	.30	.15	.48	.58	.90
Average clutch size	3.0	3.0	2.7	2.6	2.8	2.5
Fledged young	unknown	47	32	63	90	10
Averaged fledged per active nest	unknown	.6	1.7	1.2	.9	.03

Blackbird populations decreasing as the water rose or fell during the season. Later in the season, *Juncus* was more suitable for nesting.

Annual fluctuation of water levels in the marsh affected the time of emergence and density of the emergent vegetation. If the water level was higher than in the previous years (e.g., 1975), the littoral area of marsh had little or no emergent vegetation since it did not have sufficient time to become established. Most of the emergent vegetation was in the deeper part of the marsh and had to grow longer before it emerged, resulting in a later nesting season. Conversely, if the marsh decreased in size from the previous year, much of what was the littoral zone became dry land and no longer supported emergents. A smaller marsh also meant a shallower one, which allowed all the emergent vegetation to emerge sooner and thus provide for an earlier nesting season.

TERRITORIES.—The changes in territory size suggest that the territories may have changed in quality with respect to nest sites and/or food (Schoener 1968, Stenger 1958, Willson 1966). Territory sizes indirectly regulate the number of nests that are built because each territorial male will have 2–5 females nesting in his territory (Willson 1966).

NESTING SUCCESS.—Nesting success is typically measured as the percent of eggs which produce fledglings (Lack 1966, Ricklefs 1969). Using this criterion, the fewer the total number of nests built by the Yellow-headed Blackbird population, the greater was the success of the active nests. The assumption is that if fewer nests are built, more energy can be devoted to each nest. Also, a low ratio of active nests to total nests is closely correlated to nest success. Thus it appears that the optimum situation for nesting success is a low number of total nests with a low proportion of them being active. But why are so many never-to-be-used nests built?

To imply that the birds actively strive to create this set of circumstances would hint at group selection, which I will not invoke as an explanation. An individual male, seek-

ing to attract as many females as possible, will attempt to establish as large a territory as it can defend and include in it as much vegetation edge as possible because females tend to be found in territories with more edge (Willson 1966). An individual female will begin to build a nest as soon as the vegetation can support a nest, but this early nesting leads to many abandoned or damaged nests. The weather is unstable early in the nesting season; storms and cold weather can damage or destroy the nests, eggs, or young. Or the nest may be made unusable by the growth of the vegetation in which it was built. The result is that many nests are abandoned and the female builds another elsewhere in the marsh. Orian's (1961) study of Red-winged and Tricolored Blackbirds demonstrated a high mortality of eggs and young, plus nest desertion. Based on the average sex ratio and the total number of nests, I estimate that each Yellow-headed Blackbird female builds two nests. The effect is that many more nests are built than are actually used. Although later nests are more likely to be used than earlier ones, they too suffer high losses.

Explanations for the negative correlations between numbers of active nests and total numbers of nests with the success of the active nests are offered here. A lower number of total nests implies that either (1) there were fewer breeding adults or (2) fewer nests were destroyed and replaced by another nest, both signifying less stringent breeding conditions. A lower number of active nests means fewer breeding adults competing. The negative correlation between a low ratio of active/total nests and fledging success can be explained by the movement of some breeding adults out of the marsh after their first breeding attempt. After most of the nests were built and incubation was well along in the active nests, the adult population declined. They apparently moved to areas along the edge of Eagle Lake which are considerably deeper (up to 5 m) and do not become suitable for nesting until mid-July, when the vegetation has emerged. Snelling (1968) found a similar drop in Red-winged Blackbird breeding populations. By this time, the marsh vegetation has grown to its maximal height. A sur-

vey of the lake's shoreline revealed that the blackbirds began to build nests at about the time hatching was occurring in the marsh.

PHYSICAL DIMENSIONS OF THE MARSH AND MORTALITY.—Predation becomes an important factor when the water level is low. The vast majority of losses of active nests in 1977 were due to raccoon predation because the average water level (.43 m) was so low that raccoons had easy access to the nesting areas. Although high water levels are disadvantageous in that they delay the nesting season, low water levels can be extremely detrimental by allowing terrestrial predators access.

Ricklefs's (1969) work on the nesting mortality of birds states that (1) marsh (and prairie) nesting birds have the highest mortality and (2) the major cause of this mortality is predation due to nest accessibility. Starvation rates are also higher than other birds because fields and marshes have more variable food supplies.

CONCLUSIONS

The data seem to imply that the reproductive strategy of Yellow-headed Blackbirds is inefficient in time and energy. But the situation reported here is probably typical, because the average numbers fledged for all nests were similar to that reported by Willson (1966).

The fact that the marsh becomes a suitable nesting habitat at least a month earlier than other nearby areas, inducing the birds to attempt to nest, probably explains the numerous unused nests. Nest, egg, and young mortality were all high, but some adults were able to bring one or two young to fledging. But whether or not the first nesting was successful, the opportunity to re-nest in the marsh or in a newly opened habitat was still available. Selection would favor those individuals which attempted to breed in an unstable environmental situation because attempting to nest early (with an apparently tenuous commitment) is probably not much riskier than self-maintenance while waiting for other areas to become suitable; the possibility of bringing off one or two young with only a slight additional risk to the individual bird would confer a

selective advantage on those individuals. Additionally, since there is no guarantee that sufficient suitable nest sites will develop later, there are selection pressures against those individuals who wait, as well as for those which nest early.

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